

**A new crayfish of the genus *Cambarus* Erichson, 1846
(Decapoda: Cambaridae) from the Cape Fear River
basin in the Sandhills of North Carolina**

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Abstract.—*Cambarus (Puncticambarus) hystricosus* is a new species of crayfish that appears to be endemic to certain streams of the Cape Fear River basin that originate in or flow through the xeric Sandhills district of the Atlantic Coastal Plain of North Carolina. It shares a number of unusual characters with *C. (P.) spicatus* Hobbs of the Broad River basin, and is in many ways similar to an undescribed *Cambarus* of the same subgenus with which it is syntopic. It is readily distinguished from these and other members of the subgenus by a combination of multiple cervical spines, hepatic spines, an obtuse to subacute suborbital angle that is almost always devoid of a tubercle or spine, and the absence of marginal spines or tubercles on the rostrum.

The crayfish whose description follows is another of the undescribed species in the complex previously subsumed under the name *Cambarus (Puncticambarus) acuminatus* Faxon, 1884 (Cooper 2001). The North Carolina populations of this complex have also been referred to as *Cambarus (Puncticambarus) sp. C* (Hobbs and Peters 1977, Cooper and Braswell 1995), since probably none are legitimately referable to *C. (P.) acuminatus*. This new crayfish is currently known only from certain streams within or near that part of the Cape Fear River basin that lies in the xeric Sandhills district of the Inner Atlantic Coastal Plain. This is a physiographically distinctive region of Eocene sediments (Pinehurst Formation) that sit atop Cretaceous strata (Middendorf Formation) at the eastern margin of the Fall Zone of the Piedmont Plateau, bordered on the east by the Orangeburg Scarp, a marine escarpment that “is generally considered to be an early Pliocene wave-cut feature.” (Cabe et al. 1992:177). In contrast to the flatness of the rest of the Coastal

Plain, the district is characterized by dissected topography, consisting of broad, discontinuous ridges and adjacent slopes. In North Carolina it is traversed by streams in parts of the Cape Fear, Lumber, and Yadkin-Pee Dee river basins. The distinguishing terrestrial floral community of the Sandhills is the *Pinus palustris/Quercus catesbyi/Aristida stricta* association. Aquatic animals known to be endemic to the district, in addition to the crayfish described herein, are the fishes *Etheostoma mariae* (Fowler), which appears to occur only in the Lumber basin, and *Semotilus lumbee* Snelson and Suttkus, which occurs in all three river basins. An undescribed salamander of the genus *Eurycea* is also endemic to the Sandhills, where it is known from in and near streams in both the Cape Fear and Lumber river basins.

Since at least one other member of the *C. (P.)* species C complex, ostensibly another undescribed species, occupies some of the same streams as the new species, no

reliable synonymy can at this time be presented.

Measurements of crayfish structures were made to the nearest 0.1 mm with a Fowler precision dial caliper, following the methods of Hobbs (1981:9–10) unless otherwise noted. Abbreviations used in the text are as follows: j, juvenile; NC, North Carolina State highway; NCSM, North Carolina State Museum of Natural Sciences, Raleigh; PCL, postorbital carapace length; R, river; SR, state secondary (county) road; TCL, total carapace length; US, United States highway; USGS, United States Geological Survey; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; UTM, Universal Transverse Mercator coordinates; and WRC, North Carolina Wildlife Resources Commission.

Cambarus (Puncticambarus) hystricosus,
new species

Fig. 1, Table 1

Diagnosis.—Body and eyes pigmented, eye large (\bar{X} adult diam 2.3 mm, $n = 21$). Rostrum with narrow, moderately elevated margins, slightly or strongly converging to base of acumen, which is not delimited by tubercles or spines; margins not constricted at base of acumen, converging and concave from there to acute or subacute, cephalo-dorsally directed apical tubercle or spine; acumen comprising 36.3 to 47.3% ($\bar{X} = 43.2\%$, $n = 26$) of rostrum length, latter constituting 21.8 to 26.9% ($\bar{X} = 22.7\%$, $n = 26$) of TCL; floor (dorsal surface) of rostrum broadly concave. Areola 3.3 to 4.9 ($\bar{X} = 4.0$, $n = 26$) times as long as broad (broader in juveniles), constituting 30.3 to 34.0% ($\bar{X} = 32.7\%$, $n = 26$) of TCL and 38.8 to 43.3% ($\bar{X} = 41.8\%$, $n = 26$) of PCL, with 5 or 6 punctations across narrowest part. Thoracic section of carapace dorsally punctate, dorsolaterally granulate, laterally cobbled with tubercles; cephalic section laterally with many tubercles, hepatic region with strong spines or spiniform tubercles.

Cervical spines strong, 2–4 each side of carapace, plus one to several tubercles. Postorbital ridge strong, cephalic margin tapered and with strong spine or acute tubercle. Suborbital angle obtuse to subacute, almost always without tubercle or spine; branchiostegal spine strong. Antennal peduncle with 2 strong spines; antennal scale 2.4–2.9 ($\bar{X} = 2.6$, $n = 24$) times as long as wide, greatest width at midlength; lateral margin thickened and terminating distally in long spine.

Palm of chela 1.5–1.8 ($\bar{X} = 1.7$, $n = 22$) times wider than deep; width of palm 1.2–1.7 ($\bar{X} = 1.4$, $n = 19$) times length of mesial margin, latter constituting 29.0–32.2% ($\bar{X} = 30.4\%$, $n = 19$) of total chela length; mesial margin with subserrate mesial row of 7–9 (usually 8) large, semierect tubercles, subtended dorsally by row of 6–8 (usually 7) tubercles of same size or slightly smaller, and other smaller but produced tubercles immediately dorsal to this row; 1–3 small tubercles ventral to mesial row. Fixed finger of chela costate laterally, with moderately developed dorsal and ventral ridges; opposable surface of finger with row of 6–9 (usually 7 or 8) tubercles, in addition to subconical tubercle ventral to denticles; dactyl length 1.8–2.3 ($\bar{X} = 2.0$, $n = 20$) times length of mesial margin of palm, with moderately to poorly developed ridges dorsally and ventrally; mesial surface of dactyl with strong tubercles on proximal half or more; opposable surface with row of 9–12 (usually 10) tubercles. Carpus with strong dorsomesial tubercles, mesial surface with massive subdistal spine, ventral surface usually with 2 strong distal spines; merus with pair of prominent subdistal dorsal spines.

Hook on ischium of third pereiopod of males, that of form I male uniramous, massive, tapered, overreaching basioischial articulation by most of length, opposed by large tubercle on basis; coxa of fourth pereiopod of males with vertically disposed, caudomesial boss.

In situ gonopods (first pleopods) of form

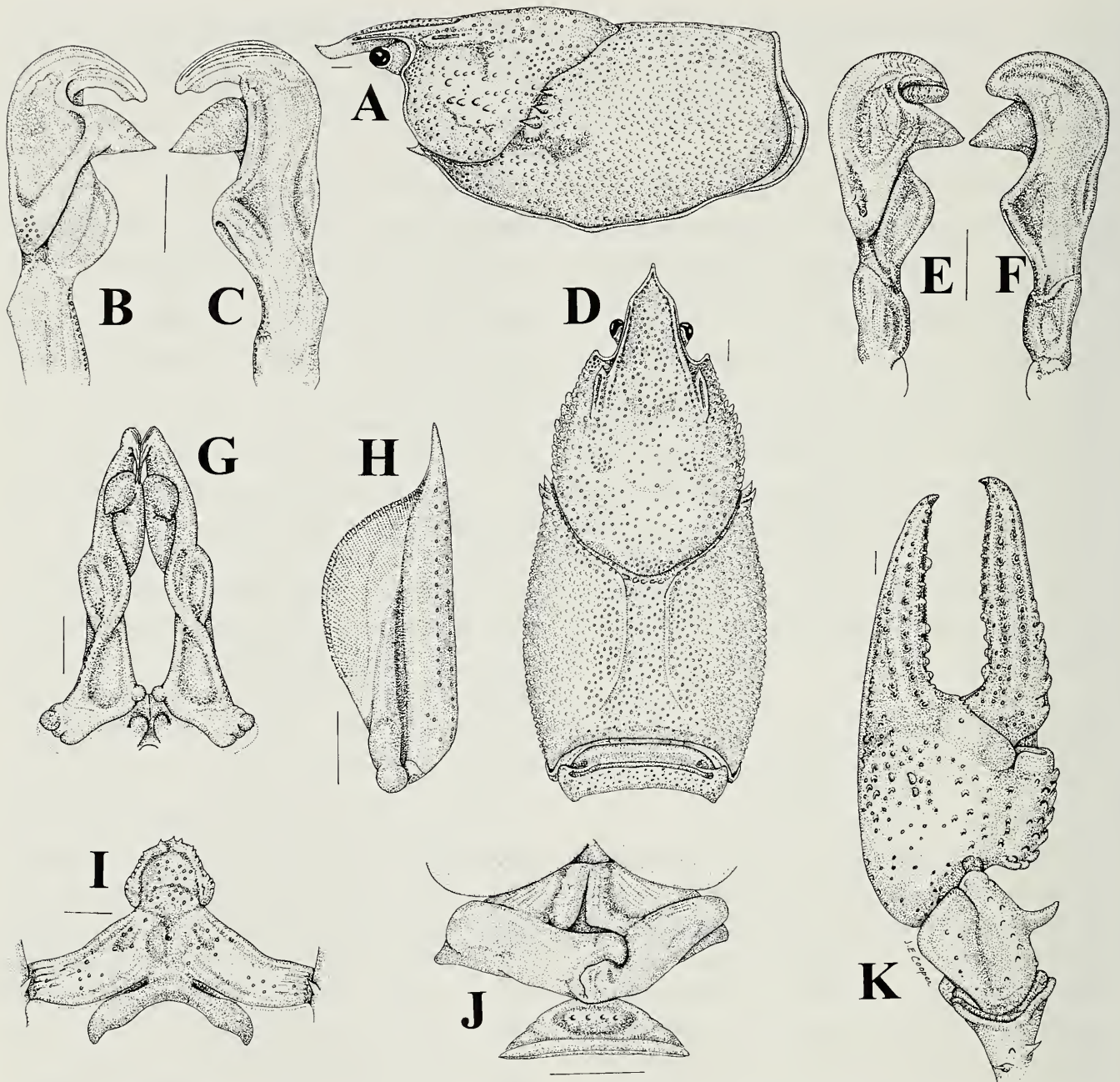


Fig. 1. *Cambarus (Puncticambarus) hystricosus*, new species. All from holotypic male, form I (NCSM 5115), except E, F, from morphotypic male, form II (NCSM 5120), and J, from allotypic female (NCSM 5004): A, lateral aspect of carapace; B, E, mesial aspect of left gonopod (first pleopod); C, F, lateral aspect of left gonopod; D, dorsal aspect of carapace; G, caudal aspect of in situ gonopods; H, right antennal scale; I, epistome; J, annulus ventralis and postannular sclerite; K, dorsal aspect of distal podomeres of left cheliped. Setae not illustrated. Scale line = 2 mm.

I male (based on holotypic male; Fig. 1G) symmetrical; proximomesial apophyses moderately developed, subglobose, slightly separated; central projection directed caudally; mesial process directed caudally and slightly laterally, with acute tip recurved caudally; in lateral aspect (Fig. 1C), central projection curved over 90° to plane of shaft, untapered, bearing proximally directed sub-

apical notch, tip not extending as far caudally as tip of mesial process; latter inflated, tapered, tip acute; distal margin convex near shaft and inclined caudoproximally, proximal margin inclined slightly caudodistally; in mesial aspect (Fig. 1B), distal portion of gonopod relatively plane, with sparse setae at midlength. Total length of gonopod 22.6% of TCL (28.3% of PCL).

Table 1.—Measurements (mm) of types of *Cambarus (Puncticambarus) hystricosus*, new species.

	Holotypic male, form I	Allotypic female	Morphotypic male, form II
Carapace			
Total length	46.8	40.7	39.7
Postorbital length	37.4	32.3	31.7
Width	24.7	20.8	20.3
Depth	14.2	13.8	14.0
Length rostrum	10.2	9.1	8.7
Length acumen	3.7	4.1	3.7
Length areola	15.9	13.2	13.1
Width areola	3.7	2.7	3.5
Antennal scale			
Length	8.9	8.6	7.9
Width	3.4	3.1	3.0
Abdomen			
Length	44.6	43.8	41.5
Width	22.0	20.2	18.6
Cheliped			
Length lateral margin chela	42.4*	28.5	31.6
Length mesial margin palm	12.3	8.9	9.5
Width palm	20.5	12.4	14.3
Depth palm	11.5	7.7	8.5
Length dactyl	27.8	17.5	19.1
Gonopod length	10.6	N/A	8.9

* Regenerated.

Annulus ventralis (based on allotypic female; Fig. 1J) about 1.6 times wider than long, subsymmetrical, subrhomboidal in shape; cephalic half depressed, sloping, with narrow median trough not dissecting cephalic margin, trough flanked each side by low ridge; dextral ridge straight, proceeding caudally to meet cephalic margin of caudodextral wall; sinistral ridge less well defined, straight, proceeding caudally to about midlength of annulus before making abrupt turn to join upper arm of reverse C-shaped caudosinistral wall; caudodextral wall fairly thick, straight, slanted about 30–35° from horizontal plane; caudosinistral wall rounded, margin directed about 55° from horizontal; transverse tongue originating from caudodextral wall, proceeding sinistrally, curving slightly before plunging into deep fossa beneath sinistral wall; sinus nearly dissecting caudal margin in midline, caudal wall with weak median labiellum.

Mirror image of this configuration present in 29 of 52 females.

Measurements of type specimens provided in Table 1.

Description of holotypic male, form I.—Body and eyes pigmented, eye 2.6 mm diameter. Cephalothorax (Fig. 1A, D) subcylindrical, thoracic section wider than deep. Areola 4.3 times longer than wide, constituting 34.0% of TCL (42.5% of PCL), quite punctate, 6 punctations across narrowest part. Rostrum with narrow margins slightly converging nearly to base of acumen, where not constricted, but more convergent and concave to apical tubercle, which reaching base of distal two-thirds of ultimate podomere of antennular peduncle; acumen comprising 36.3% of rostrum length, latter constituting 21.8% of TCL; floor of rostrum broadly concave, proximal three-fourths of surface punctate; usual row of deep punctations along inner surface of dorsal ridge;

subrostral ridge weak, narrowly visible to base of acumen in dorsal aspect; ventral keel of rostrum devoid of tubercles or spines.

Postorbital ridge strong, straight, laterally grooved, cephalic margin with acute tubercle, caudal terminus somewhat inflated. Suborbital angle rounded, without spine or tubercle; branchiostegal spine strong. Thoracic section of carapace dorsally punctate, dorsolaterally granulate, laterally cobbled with tubercles; row of small tubercles along ventral margin of anterior part of cervical groove; cephalic section of carapace 1.9 times longer than areola, constituting 66.0% of TCL, laterally covered with small to large tubercles, most acute or subacute; gastric region punctate. Cervical spine region on each side of carapace with 2 strong spines, 1 smaller spine dorsal to them, and some tubercles.

Abdomen slightly narrower and shorter than cephalothorax; abdominal pleura truncate ventrally, subangular caudoventrally, slightly rounded caudally; terga very punctate, except articular surfaces glabrous. Proximal podomere of uropod with spine on lateral lobe, larger spine on mesial lobe; mesial ramus of uropod with weak median ridge bearing submarginal caudomedian spine; caudolateral spine of ramus moderate; cephalic section of lateral ramus of uropod with broad, curved median ridge bearing terminal spine at transverse flexure, latter on right with total of 14 fixed spines and 1 long, articulated sublateral spine along caudal margin. Telson with 2 strong spines in each caudolateral corner of cephalic section, mesialmost articulated (tip of fixed spine on left side bifurcate); caudal margin domelike.

Epistome (Fig. 1I) with cephalic lobe basically subcordiform in ventral outline, but cephalic margin slightly curved, not peaked, and lateral margin on each side with weak concavity; most of margin crenulate, with tuberclelike protuberances; lateral corners inflated; floor (ventral surface) of lobe moderately convex, punctate, with setae;

central depression of body broad, deep, with cephalomedian fovea; lamellae punctate, lateral corners subtruncate, without tubercles; zygotoma moderately arched. Antennal peduncle with strong cephalolateral spine on basis, similar spine on ventral surface of ischium; antennular peduncle with small subdistal median spine on ventral surface of basal podomere. Antennal scale (Fig. 1H) 2.6 times longer than wide, broadest near midlength; lateral margin thickened, straight, terminating in long distal spine, tip of which reaching midlength of ultimate podomere of antennular peduncle; lamella about 1.5 times as wide as thickened lateral margin, with declivous distal margin and broadly curved mesial margin.

Third maxilliped with tip reaching slightly beyond midlength of penultimate podomere of antennal peduncle; exopodite hirsute, tip reaching nearly to midlength of merus of endopodite; distolateral corner of ischium produced as acute tubercle; lateral half of ischium with some punctations, short setae present along inner margin of lateral ridge; mesial half of ischium with eroded bristles, mesial margin on right with 21 denticles, 22 on left. Incisor ridge of right mandible with 6 denticles, 5 on left.

Both chelipeds regenerated (left more nearly normal; deviations noted in following). Left chela (Fig. 1K) 2.1 times longer than wide; palm 1.8 times broader than deep, width 1.7 times length of mesial margin (normal range 1.2–1.7, \bar{X} = 1.4); latter 29.0% of total chela length, 44.2% of dactyl length. Dorsal surface of palm punctate, those punctations on mesial third with small tubercles at proximal bases; longitudinal dorsomesial sulcus shallow, with row of moderate, produced tubercles; distolateral margin of palm costate for about a third of length (continuous onto fixed finger), with moderate impression and aggregation of large punctations with tubercles at proximal bases; lateral eminence of articular ridge with several small distal protuberances; lateral margin of palm rounded, with large,

widely spaced punctations. Ventral surface of palm less punctate than dorsal, some punctations on mesial half with minuscule basal tubercles; distolaterally with broad depression (continuous onto fixed finger) and scattered punctations without tubercles; lateral eminence of articular ridge with 1 subdistal tubercle and 1 distal protuberance; 2 tubercles proximal to ridge. Mesial margin of left palm with subserrate mesial row of 8 tubercles, row subtended dorsolaterally by row of 6 tubercles, and others dorsal to this row; 2 tubercles ventral to mesial row.

Fingers gaping most of length, greatest width of gape about equal to width of base of dactyl. Left fixed finger costate laterally; dorsal surface with moderately strong longitudinal median ridge, flanked each side by row of punctations; proximolateral area with moderate impression and large punctations, some with basal tubercles; lateral margin with row of large punctations; ventral surface with weak, rounded longitudinal ridge, flanked each side by row of punctations; opposable margin with usual subconical tubercle (worn) ventral to denticles, located at base of distal fourth of finger, and another smaller ventral tubercle distal to subconical one (abnormal); row of 11 tubercles dorsal to denticles (normal range 6–9, usually 7 or 8), first of these very small, fifth from base largest; denticles eroded, in 2 rows distally. Dorsal surface of dactyl with low ridge, flanked each side by row of punctations; mesial surface with strong tubercles on proximal half, basal tubercles in 2–3 rows, encroaching dorsally; ventral surface with obsolete longitudinal ridge, defined by 2 rows of punctations; opposable surface with 13 tubercles (normal range 9–12, usually 10), first and fourth from base largest; denticles eroded, in 2 rows on distal third of finger.

Left carpus (Fig. 1K) 1.4 times as long as wide, 1.3 times as long as mesial margin of palm; dorsal surface of carpus with shallow, oblique sulcus, lateral to which surface punctate, mesial to which surface with 8 or 9 dorsomesial tubercles; mesial margin with

stout, curved distal spine and minuscule proximal tubercle; ventral surface with 2 strong distal spines (tip of distolateral spine broken) and 1 proximomesial tubercle. Left merus 1.7 times longer than deep, dorsal surface with 2 strong, suberect subdistal spines and 1 minuscule tubercle; ventrolateral ridge with 1 small tubercle, 2 stout spines, and moderate distal spine; ventromesial ridge with 4 subacute tubercles, 4 spines, and broken distal spine; ischium with 5 small ventral tubercles.

Gonopods as described in "Diagnosis."

Description of allotypic female.—Except for secondary sexual characters, differing from holotypic male in following respects: Areola 4.9 times wider than long, constituting 32.4% of TCL (40.9% of PCL), with 4 or 5 large punctations across narrowest part. Acumen long, spiniform, comprising 45.1% of rostrum length, tip reaching mid-length of ultimate podomere of antennular peduncle; rostrum comprising 22.4% of TCL; subrostral ridge narrowly visible only along proximal half of rostrum. Cephalic margin of postorbital ridge with strong spine. Cephalic section of carapace 2.1 times longer than areola, constituting 67.6% of TCL; hepatic region with spiniform tubercles. Cervical spine region on left side of carapace with 1 long spine, 2 smaller spines dorsal to it, and several tubercles; right side with 2 long and 1 small spine.

Telson with 1 fixed and 1 articulated spine in caudolateral corner of cephalic section on right, 1 fixed and 2 articulated spines on left, all spines strong.

Floor of cephalic lobe of epistome with long setae; lamellae with single caudal tubercle each corner. Antennal scale 2.8 times longer than wide; lamella about 1.2–1.3 times as wide as thickened lateral margin. Third maxilliped with cephalolateral corner of ischium produced as spine.

Both chelipeds appear normal. Right chela 2.3 times longer than wide; palm 1.6 times broader than deep, width 1.4 times length of mesial margin, which is 31.2% of total chela length and 50.9% of dactyl

length. Lateral eminence of ventral articular ridge with subacute distal tubercle; single tubercle proximal to ridge. Mesial margin of palm with staggered mesial row of 7 tubercles, row subtended dorsolaterally by staggered row of 8 tubercles (6 on left), and several small tubercles dorsal to this row. Fingers only slightly gaping in proximal half, opposable base of fixed finger with sparse long setae. Opposable surface of right fixed finger with small subconical tubercle ventral to denticles at base of distal fourth of finger, and row of 8 tubercles dorsal to denticles, fourth tubercle from base largest (on left finger, third and fourth from base largest and same size). Mesial surface of right dactyl with strong tubercles on proximal two-thirds of finger; opposable surface with 11 tubercles, basalmost one largest, fourth from base offset ventrally (left dactyl with 12 tubercles).

Dorsal surface of carpus with row of 5 dorsomesial tubercles; mesial surface with long, curved spine at about midlength, no proximal tubercle. Right merus 1.9 times longer than deep; ventrolateral ridge with 3 strong spines; ventromesial ridge with 8 spines or spiniform tubercles (7 on left merus) and strong distal spine.

Annulus as described in "Diagnosis." In addition, first pleopods present, fairly long; postannular sclerite about one-third width of annulus, ridgelike, ventral surface pitted.

Description of morphotypic male, form II.—Differing from holotypic male in following respects: Areola 3.7 times longer than wide, constituting 33.0% of TCL (41.3% of PCL). Acumen comprising 42.5% of rostrum length. Cephalic margin of postorbital ridge with strong spine. Cephalic section of carapace with several strong hepatic spines on each side of body. Cervical spine area with 3 spines and a tubercle.

Cephalic lobe of epistome subcordiform in outline, margins crenulate, with some short setae; floor plane, with setae. Tip of spine of antennal scale reaching distal margin of ultimate podomere of antennular pe-

duncle; lamella about 1.6 times width of thickened lateral margin. Incisor ridge of right mandible with 7 denticles.

Right cheliped replaced by regenerating bud. Left chela 2.2 times longer than wide; palm 1.7 times broader than deep, width 1.5 times length of mesial margin; latter 30.1% of total chela length, 49.7% of dactyl length. Lateral eminence of ventral articular ridge with 2 distal tubercles; 2 tubercles proximal to ridge. Mesial margin of palm with subserrate mesial row of 7 tubercles, row subtended dorsolaterally by staggered row of 7 tubercles, and others dorsal to this row; 2 produced tubercles ventral to mesial row. Fingers gaping in proximal three-fourths of length, greatest width of gape about four-fifths width of base of dactyl. Dorsal surface of fixed finger with strong median ridge, flanked mesially by punctate groove; opposable margin with strong subconical tubercle ventral to denticles, and row of 8 tubercles dorsal to denticles, fourth tubercle from base largest. Opposable surface of dactyl with 12 tubercles, basalmost largest. Mesial surface of carpus with long, curved subdistal spine and small proximal tubercle; ventral surface with 2 strong distal spines and large proximomesial tubercle. Merus 1.8 times longer than deep; ventrolateral ridge with 3 strong spines and moderate distal spine; ventromesial ridge with 4 small tubercles and 6 spines.

Hook on ischium of third pereopod small, tuberclelike, not overreaching basioischial articulation, not opposed by tubercle on basis. Gonopod (Fig. 1E, F) length 22.4% of TCL (28.1% of PCL). In situ gonopods with small, separated proximomesial apophyses; central projection directed caudally; mesial process inflated, directed caudolaterally and inclined slightly proximally; in lateral aspect, central projection curved 90° to plane of shaft, broad, tapered; mesial process tapered, tip slightly extruded.

Color notes.—Ground color of carapace and abdomen (except tailfan) gray-green to olive. Thoracic section of carapace with

large, pale greenish blotches, one such blotch in median third of carapace at caudal end of areola; laterally darker, with small, light blotches and white granules; cervical spines ivory or roseate. Cephalic section of carapace nearly uniform olivaceous dorsally, darker laterally, with large tan or whitish blotch along cephalolateral margin between suborbital area and white branchiostegal spine; hepatic spines and tubercles on lateral surface white. Postorbital ridge pale grayish-green, cephalic spine tan to yellowish. Antennal scale bluish, but mesial margin of thickened lateral portion tan; antennal and antennular flagellae variable in color, with dark brown, reddish tan, or tan articles, and brown or pale green interstices.

Dorsal surfaces of palm and fingers of cheliped blue-green; lateral margin of entire propodus creamy orange, or yellowish with blue-gray areas; ventral surfaces of palm and fingers pale grayish-green or blue-green, but mesial third of palm and most of dactyl usually darker; tips of fingers orange or tannish-orange, color not subtended by black band; tubercles on mesial margin of palm and dactyl pale green, tubercles on opposable surfaces of both fingers ivory, pale green, or blue-gray. Dorsal and mesial surfaces of carpus gray-green, dorsal tubercles same color but paler; proximal and distal margins of carpus with narrow russet band. Dorsal surface of merus gray-green on distal half, fading to white on proximal half, distal membrane blue, spines ivory; ventral merus nearly white, spines white with amber tips; proximal two-thirds of mesial surface ivory, darker on distal third; lateral surface white. Dorsal surfaces of second through fifth pereopods pale greenish-blue or blue, articulations brownish; fingers of chelae of second and third pereopods blue with amber tips.

Abdominal terga grayish-green, caudal margin of each with transverse black or iodine band, which broader on cephalicmost tergite; latter also with pale (usually yellowish) blotch at each lateral terminus; pleura generally darker green with bluish over-

tones, each with large, diagonal yellowish or tannish blotch near ventral border and dark oblique dorsolateral mark. Telson and uropods aquamarine dorsally and ventrally, dorsal surface of telson with tan overtones; both rami of uropods with narrow transverse subcaudal band of orange-tan, subtended caudally by narrow blue band; transverse flexure of lateral ramus of uropod also with narrow orange-tan band.

Ventrally, all cephalic structures of body blue-green or bluish, except zygoma white, and mandible and parts of third maxilliped lighter in color, sometimes pale yellowish; other ventral surfaces of body white or translucent blue, ventral abdomen usually with blue markings.

Juveniles with same general pattern, but paler. Ventral margins of carapace often distinctly blue; dorsal abdomen pale greenish, terga with very prominent dark banding.

Type locality.—North Carolina, Hoke County, Puppy Creek at SR 1409, ca. 2.4 air km E of Wayside (Nicholson Creek 7.5' USGS quadrangle, UTM Zone 17, coordinates 670662E/3876690N).

Disposition of types.—The holotypic male, form I, allotypic female, and morphotypic male, form II, are in the NCSM crustacean collection (catalogue numbers 5115, 5004, and 5120, respectively), as are paratopotypes consisting of 3j♂, 3j♀ (5055); 2♀ (5060); 1♀ (5117); 1♂ II (5119); 4j♂, 2j♀ (5118); 1♀ (5254); 1j♂ (5288); 5j♂, 3j♀ (6206); and paratypes consisting of 1♂ II, 1♀ (2524); 1♂ II, 2j♂, 2♀, 2j♀ (6371); 9j♂, 1♀, 8j♀ (5057). Paratypes consisting of 1♂ II, 4j♂, 4♀, 5j♀ have been deposited at USNM (1004633).

Range and specimens examined.—North Carolina endemic; currently known from twelve creeks in the Rockfish Creek and Little River subdrainages, and one creek that forms an independent subdrainage, of the Cape Fear River basin in and near the Sandhills district of the Atlantic Coastal Plain. More than 250 voucher specimens have been collected from the following localities (collectors names given in first use-

- age, initials thereafter): *Cumberland Co.*—(1) upper trib Bones Crk at SR 1400; 1 ♂ II, 1 ♀ (2524), 30 Jan 1989, coll. T. MacPherson, D. R. Lenat (DRL); (2) Little Rockfish Crk at SR 1102 (Gillis Hill Rd); 2 j♂, 1 j♀ (WRC 000830.1jaj), 30 Aug 2000, coll. B. T. Watson (BTW), A. H. Fullerton (AHF), J. A. Johnson (JAJ); (3) Little Rockfish Crk at Cameron Rd; 1 j♀ (WRC 001031.4jaj), 31 Oct 2000, coll. BTW, AHF; (4) Rockfish Crk at boundary Fort Bragg Military Reservation (35.08.04N/79.21.06W); 1 ♂ II (2716), date unknown, coll. P. W. Havens (PWH); (5) Stewarts Crk at SR 1102 (Gillis Hill Rd); 1 intersex adult (6395), 30 Aug 2000, coll. BTW, AHF, JAJ; (6) Grays Crk at SR 2234 (Blossom Rd), ca. 3.7 air km W of Lena; 1 ♂ I, 2 ♂ II, 6 j♂, 3 ♀, 2 j♀ (23584), 31 Oct 2000, coll. AHF, BTW. *Hoke Co.*—(7) Horse Crk, Fort Bragg Military Reservation (35.11.30N/77.12.00W); 1 ♂ II (2712), date unknown, coll. PWH; (8) Rockfish Crk at US 401 Bypass, 2.7 km NE of Raeford; 1 ♂ II, 2 j♂, 2 ♀, 2 j♀ (6371), 26 Oct 2000, coll. W. C. Starnes, M. Raley, G. Hogue, L. Fullbright; (9) Rockfish Crk, 3.2 km N of Raeford; 1 ♂ I (5255), 9 Jul 1962, coll. D. Louder; (10) Rockfish Crk at firebreak 32 off Moore County road, Fort Bragg Military Reservation, 13.0 air km NW of Raeford; 2 j♂, 1 j♀ (23873), 20 Aug 2002, coll. C. Bryan (CB), A. Young (AY); (11) Puppy Crk at SR 1406, ca. 4.8 air km W of center town Rockfish; 1 j♂ (5006), 3 Feb 1999, coll. D. G. Cooper (DGC), D. A. Jackan (DAJ); 9 j♂, 1 ♀, 8 j♀ (5057), 1 j♂ (5061), 21 Mar 1999, coll. DGC, DAJ; 2 ♂ II, 3 ♀ (4993), 1 ♂ II (5120), 21 May 1998, coll. M. Hale, DRL, N. Medlin, B. Tracy (BT); (12) Puppy Crk at SR 1409 (type locality), ca. 2.4 air km E of Wayside; 2 ♀ (5060), 1 ♀ (5254), 3 j♂, 3 j♀ (5055), 26 Mar 1999, coll. DGC, DAJ; 1 ♀ (5117), 1 ♂ II (5119), 4 j♂, 2 j♀ (5118), 1 ♂ I (5115), 3 Jun 1999, coll. DGC; 1 j♂ (5288), 4 Nov 1999, coll. DGC; 5 j♂, 3 j♀ (6206), 9 Sep 2000, coll. DGC, S. Yirka; 1 ♀ (5004), 3 Feb 1999, coll. DGC, DAJ; (13) Rockfish Crk at firebreaks 3–5, Fort Bragg Military Reservation, ca. 8 air km NNW of Raeford; 1 ♂ II, 4 j♂, 4 ♀, 5 j♀ (USNM 1004633), 5 Nov 2001, coll. CB, B. Ball (BB); 1 ♂ II, 5 j♂, 11 j♀ (7990), 6 Nov 2001, coll. CB, BB; 2 j♂, 6 j♀ (23582), 7–8 Nov 2001, coll. CB, BB; (14) Little R, ca. 11.2 air km SE of Vass; 2 ♀ (7985), 25 Oct 2001, coll. CB, AY; (15) Rockfish Crk at Sandy Grove Church Rd, ca. 8 air km NNW of Raeford; 1 j♂ (23583), 5 Nov 2001, coll. CB, BB; 4 j♂, 2 ♀, 11 j♀ (23791), 9 Aug 2002, coll. CB, AY; (16) Piney Bottom Crk at Southern Pines Rd, ca. 15.5 air km NNW of Raeford; 1 ♂ II, 1 j♂ (23781), 24 Sep 2002, coll. CB, AY; (17) Gum Branch at Chicken Rd, ca. 12.4 km NNW of Raeford; 1 ♀ (23777), 24 Sep 2002; 1 j♂ (23776), 6 Sep 2002, coll. CB, AY; (18) Juniper Crk at Chicken Rd, 12.3 air km NNW of Raeford; 1 ♀ (23868), 7 Oct 2002, coll. CB, AY; (19) Juniper Crk at firebreak 13, Fort Bragg Military Reservation, 10.6 air km NNW of Raeford; 1 ♀ (23864), 1 Nov 2002; 1 ♂ II, 2 j♂, 3 j♀ (23829), coll. CB, AY; (20) Juniper Crk at firebreak 29, Fort Bragg Military Reservation, 7.7 air km NNW of Raeford; 3 ♂ II, 9 j♂, 5 ♀, 14 j♀ (23867), 1 Oct 2002; 2 ♂ I, 1 ♂ II, 1 j♂, 14 j♀ (23827), 1 Nov 2002, coll. CB, AY; (21) Juniper Crk at Plank Rd, 8.8 air km NNW of Raeford; 1 ♂ II, 5 j♂, 1 ♀, 4 j♀ (23865), 23 Sep 2002; 1 ♂ II (23866), 1 Nov 2002, coll. CB, AY; (22) Nicholson Crk at firebreak 15, Fort Bragg Military Reservation, 10.4 air km N of Raeford; 1 ♂ II, 2 j♂, 1 ♀, 6 j♀ (23869), 20 Oct 2002; 2 ♂ II, 2 j♂ (23870), 1 Nov 2002, coll. CB, AY; (23) Nicholson Crk at firebreak 29, Fort Bragg Military Reservation, 6.9 air km N of Raeford; 4 ♂ II, 6 j♂, 2 ♀, 3 j♀ (23871), 19 Oct 2002, coll. CB, AY; (24) James Crk at boundary road, Fort Bragg Military Reservation, 6.4 air km SSW of Vass; 1 j♂ (23872), 2 Nov 2002, coll. CB, AY. *Moore Co.*—(25) Nicks Crk at NC 22, ca. 3.7 air km W of Whispering Pines; 1 ♂ II, 2 ♀, 1 j♀ (3308), 31 May 1996, coll. DRL, BT.

Variations.—In addition to those ad-

dressed elsewhere in this paper, intraspecific variations include the following. The degree of convergence of the margins of the rostrum, from its base to the base of the acumen, varies from subparallel to strongly convergent, and in some individuals the rostrum is nearly caret-shaped. Although the floor of the rostrum is usually moderately concave, in some specimens it approaches being plane. The suborbital angle is obtuse (very seldom subacute or obsolete) and only rarely bears a tubercle or small spine. Six specimens show disparities in this character from one side of the carapace to the other, displaying varying combinations of obtuse or subacute angles with or without tubercles. The hepatic ornaments vary from strong spines to subacute tubercles, and are weak, if present, in the sample from Grays Creek, a small, independent subdrainage of the Cape Fear River at what appears to be the southernmost periphery of the range of specimens assignable to *C. (P.) hystricosus*.

In about half the specimens examined the distal margin of the lamella of the antennal scale is subtransverse for about half its width before curving proximomesially, while in the others this margin is gently or moderately declivous from the base of the spine to the widest part of the scale at about midlength. In nearly all specimens the shape of the cephalic lobe of the epistome is subcordiform or subtriangular, but in a few it approaches subpentagonal or semi-circular. The margins of the lobe are almost always strikingly crenulate, bearing from several to many subacute protuberances, but in a few specimens the margins are only moderately uneven. The carpus usually has from three to eight moderate or strong dorsomesial tubercles, but in some specimens these tubercles are weak, and they are fewest and weakest in the sample from Grays Creek. The mesial surface of the carpus normally lacks a proximal tubercle, but this is present in a number of specimens, and others have two or three very small tubercles at this site. The usual ventral armature

of the carpus consists of two strong distal spines, but in four specimens the distomesial spine is weak or obsolete, and in three others it is reduced to a rounded tubercle, with or without an acute nipple. The dorsal surface of the merus almost always bears two strong subdistal spines, and occasionally these may be accompanied by from one to several small tubercles. Two specimens have three strong subdistal spines on the dorsal merus. The ventrolateral ridge of the merus usually bears two or three spines, plus a strong or moderate distal spine. In some specimens there may be an additional tubercle or two on this ridge, and in several individuals the distal spine is small. The ventromesial ridge of the merus may have from six to nine ornaments, a combination of acute tubercles and moderate spines, along with a strong distal spine.

The largest tubercle on the opposable surface of the dactyl is usually the first from the base, but often is the second and occasionally the fourth; the fourth tubercle is always displaced toward the ventral surface, and not infrequently lies distinctly ventral to the denticles. The largest tubercle on the opposable surface of the fixed finger (not counting the usual subconical tubercle that lies ventral to the denticles) is generally the fourth from the base, occasionally the third or fifth.

Nearly all specimens have two spines in each cephalolateral corner of the telson, but eight have three in one corner and two in the other, six have three spines in each corner, and three have two in one corner and one in the other.

Anomalies.—In a subadult female from Puppy Creek, the distance between the base of the acumen and its apex is greater on the right side than on the left, and the base of the acumen on the right side is delimited by a strong, laterally directed spine. A juvenile male from Rockfish Creek has a deformed, probably regenerated, rostrum with a long, cephalolaterally directed spine projecting from the left side near the base. These are the only individuals in which a “marginal

spine" has been observed. A juvenile female (9.4 mm TCL) from Rockfish Creek has a small fixed spine projecting from the base of the lateral side of the regular fixed spine on the right side of the telson.

A female from Rockfish Creek lacks oviduct apertures. An adult animal (TCL 43.7 mm) from Stewarts Creek is gynandromorphic. It has a normal annulus ventralis, female first and second pleopods, and postannular sclerite, but lacks oviduct apertures in the coxae of the third pereopods. It has male sperm duct openings in the coxae of the fifth pereopods.

Size.—The largest specimen is a female measuring 52.6 mm TCL (43.0 mm PCL). The largest form I male measures 46.8 mm TCL (37.4 mm PCL); the only other form I males have TCLs of 30.8, 35.0, and 38.0 mm (25.4, 27.7, and 30.2 mm PCL, respectively). The largest form II male measures 39.7 mm TCL (31.7 mm PCL).

Life history and ecological notes.—Form I males were found in early June and July, and in October and November. No ovigerous females or those with attached young have yet been seen.

On 21 May 1998, Puppy Creek was a "clear blackwater stream with a white sand bottom" (B. Tracy, pers. comm.). Specific conductance on that date was 18 μ mhos/cm, pH 4.9, water temperature 22°C, and dissolved oxygen content 6.9 ppm. In February and March 1999, the creek at the type locality was about 3 m wide, with fairly shallow water and a few deeper sections. The bottom was sandy, with some sticks and detritus, several large submerged logs, and dense growths of long, slender submerged vegetation in which the crayfish were found. At some points the banks were undercut and covered with overhanging roots, but passing a dipnet through these produced no crayfish. In June of the same year, water levels had dropped significantly, the vegetation was not completely submerged, and the few crayfish collected were found only among sticks and detritus in areas with the greatest current.

Other members of the aquatic community at the type locality included the fishes *Ameiurus* sp., *Aphredoderus sayanus* (Gilliams), *Enneacanthus chaetodon* (Baird), *Etheostoma olmstedii* Storer, *E. serrifer* (Hubbs and Cannon), *Lepomis gulosus* (Cuvier), *Notropis cummingsae* Myer, and *Noturus insignis* (Richardson); the neotenic salamander *Necturus punctatus* (Gibbes); and the watersnake *Nerodia taxispilota* (Holbrook).

Crayfish associates.—The only other crayfishes yet found at sites occupied by *C. (P.) hystricosus* are an undescribed member of the subgenus, and *Procambarus (Ortmannicus) acutus* (Girard, 1852). *Cambarus (Depressicambarus) latimanus* (LeConte, 1856) occurs in some other streams of the area, but has not yet been found in those occupied by *C. (P.) hystricosus*.

Affinities.—On the basis of its extensive spinal armature, which we consider a plesiomorphic character state (and see Hobbs 1962:276, 1969:116–118), *C. (P.) hystricosus* appears to have strong affinities with *Cambarus (Puncticambarus) spicatus* Hobbs, 1956. Both species characteristically have hepatic spines, or strong spiniform or very acute tubercles, a rare feature in epigeal *Cambarus*; strong cervical spines that are multiple in *C. (P.) hystricosus* and sometimes so in *C. (P.) spicatus*; long branchiostegal spines; and strong, multiple spines on the antennal peduncle, ventral carpus, and dorsal and ventral merus. Major differences between the two species are the presence of marginal spines or strong tubercles on the rostrum of *C. (P.) spicatus*, which are never normally present in *C. (P.) hystricosus*; a spine or tubercle on the suborbital angle of *C. (P.) spicatus*, which is rarely seen in *C. (P.) hystricosus*; the structure of the central projection of the form I male gonopod, which in *C. (P.) spicatus* is scarcely curved beyond 90° to the shaft and has a very weak subapical notch; and the more symmetrical annulus of that species.

The other member of the subgenus that occurs in some streams with *C. (P.) hystri-*

cosus lacks hepatic spines and multiple cervical spines, although it may display acute or subacute cervical tubercles along with a single strong spine. The suborbital angle in this species is almost always acute or subacute and bears a tubercle or spine. Only two of forty-five specimens examined had an obtuse suborbital angle, and in only one of them did the angle lack a tubercle. The postorbital ridge of adults seldom bears more than a small cephalic tubercle, although some smaller specimens have a cephalic spine. This species also has a shorter acumen and a broader areola than *C. (P.) hystricosus*, and the base of its acumen is more angular.

Remarks.—Both *C. (P.) hystricosus* and *C. (P.) spicatus* occupy limited, circumscribed ranges, the former in streams of the Cape Fear River basin in the Sandhills of North Carolina, the latter in streams of the Broad River basin in the Piedmont Plateau of North and South Carolina. The ranges of both are surrounded by the ranges of other, presumably more derived, members of *Puncticambarus*. In the Sandhills, this is comparable to the distributions of two other endemic animals. Populations of *Semotilus lumbee* there are surrounded by its more broadly distributed relative, *Semotilus atromaculatus* Mitchill, and populations of the undescribed *Eurycea* are surrounded by its close relative, *Eurycea cirrigera* (Green).

It seems reasonable that the forerunner of *C. (P.) spicatus* and *C. (P.) hystricosus* was one of the few members of the genus *Cambarus* to expand its range eastward from the Blue Ridge escarpment—which then lay farther east than it does today—or from farther west. Colonization of the Piedmont Plateau and the eastern extremity of the Inner Coastal Plain would have met with little opposition, but continued eastward expansion would have brought this putative progenitor into conflict with procambaroid stocks. The latter crayfishes were adapted to the warm, lentic or low-gradient habitats of the broad, base-leveled Coastal Plain, habitats that likely would have been inim-

ical to exploitation by more cold- and lotic-adapted cambaroid stocks. The later radiation into the Piedmont of more highly competitive and closely related forms could have fragmented the ranges of the earlier inhabitants into a number of allopatric populations that evolved into distinctive relicts. Other such populations may await discovery.

The “residual” genetic influences of a once widespread, presumably plesiomorphic *Puncticambarus* could help explain the occasional appearance of hepatic spines, marginal spines, and even instances of multiple cervical spines, observed in some individuals from a number of populations of more derived forms in the subgenus (JEC, pers. obs.).

Etymology.—Species *hystricosus*, meaning prickly, from the Latin *hystrix*, porcupine, in reference to its extremely spinose body parts.

Suggested vernacular name: Sandhills spiny crayfish.

Acknowledgments

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